APPENDIX I: STUDY SPECIES AND FIELD METHODOLOGY

STUDY SPECIES:

General Ecology:

Lemurs are *Strepsirrhini* primates (prosimians), making them an evolutionarily distinct lineage from apes and monkeys. Ringtailed lemurs, *Lemur catta*, like all members of the *Lemuridae* family, are endemic to Madagascar. They are found in a variety of habitats in the southern tip of the island but their populations are densest in gallery forests (Sauther 1992). Ringtailed lemurs are considered to be opportunistic omnivores, eating a wide variety of food items including fruits, leaves, leaf stems, flowers, flower stems, spiders, spider webs, caterpillars, cicadas, insect cocoons, and birds (Sauther 1992). In addition, ringtailed lemurs are known to be both highly arboreal and terrestrial, which allows them to take advantage of habitats and food items that other lemur species cannot (Sauther 1992). As a result, ringtailed lemurs are considered to be behaviorally flexible and are known to be able to rebound well from environmental perturbations (Gould *et al.* 1999).

Reproductive Ecology:

This species has a highly constrained breeding period lasting only 6-24 hours per year (Jolly 1966), with all females going into estrus within one to three weeks of one another (Sauther 1991). Females mate polygamously with resident males, transfer males, and neighboring males, in that order (Jolly 1966, Sussman 1992, Gould 1994).

Approximately 80-85% of females give birth each year (Sussman 1991). The birthing period and lactation frequently coincide with a peak in fruit availability (Rasamimana & Rafidinarivo 1993). Newborn infants are carried on their mother's stomach and switch to her back as they get older. They are weaned at four to five months of age (Sauther *et al.* 1999), at which point, most carrying and suckling ceases. The infant mortality rate in the first year is between 30% and 51% (Sussman 1991). Infanticidal behavior has rarely been observed in this species and females do not increase agonism towards males during the period of lactation when the infants are most vulnerable (Gould 1990, Gould 1992, Sauther & Sussman 1993).

Social Behavior:

Ringtailed lemurs live in the largest and most complex social groupings of all prosimians (Jolly 1966). They live in multi-male female resident groups of between 9 and 22 individuals (Sussman 1991). Ringtailed lemur sociality is characterized by female philopatry and male migration (Sussman 1992, Gould *et al.* 1999), female social dominance (Kappeler 1990a, b, Sauther 1992) and the formation of variable dominance hierarchies (Pereira & Kappeler 1997). Among females, these hierarchies can be despotic (Pereira & Kappeler 1997) or linear, and stable over time (Sauther 1992). However, social relationships are known to change abruptly resulting in occasionally unstable and non-linear hierarchies (Sterck *et al.* 1997). Unlike cercopithecine primates, who also form despotic and linear hierarchies, ringtailed lemur daughters do not rank immediately below their mothers (Nakamichi & Koyama 1997). This is likely because mothers do not offer consistent coalitionary support to their offspring (Pereira 1995). In

fact, coalition formation is considered to be very rare among ringtailed lemurs (Nakamichi & Koyama 1997). Males, on the other hand, generally lack a consistent linear hierarchy and experience frequent rank reversals (Gould 1994). Mature males migrate out of their social group every 3.5 years on average (Sussman 1992). When a group reaches a critical size, a process of episodic and targeted aggression may occur, often resulting in fission along matrilineal lines (Sussman 1991, 1992, Hood & Jolly 1995). This results in the expulsion of individuals, thus allowing previous levels of aggression to resume.

Sterck *et al.* (1997) classified ringtailed lemurs as a dispersal-egalitarian species (Figure 2). However, Erhart and Overdorff (2008) found that their social characteristics do not fit into any of the socioecological model's existing categories explaining female social relationships, although they can most closely be categorized as a resident-nepotistic species. The manner in which their social structure is currently understood predicts that this species will encounter high frequencies of unidirectional aggression and low frequencies of reconciliation (Kappeler 1993). However, Gould (1996) and Sussman *et al.* (2003) found that ringtailed lemurs spent extremely little time in agonistic interactions and that these events were usually mild. The "reconciliatory" tendencies of ringtailed lemurs remain unclear, with most evidence pointing towards the absence of this suite of behaviors. Kappeler (1993) found no indication of reconciliation in the 10 minutes following a fight. Conversely, Rolland and Roeder (2000) found "reconciliation" when using an hour post-conflict period. Similarly, Palagi *et al.* (2005) looked at reconciliation in two groups of ringtailed lemurs and found that while the

frequency and intensity of agonistic interactions were not significantly different, only one group exhibited reconciliation.

Communication:

Ringtailed lemurs use 28 distinct vocalizations, six of which are specific to juveniles (Macedonia 1993). Some of the most common calls are listed in table 7. They include affiliative, agonistic, submissive, and predator vocalizations. See Macedonia (1993) for a complete description and interpretation of ringtailed lemur vocalizations. Ringtailed lemurs also rely on chemical communication. Females and males have anogenital scent glands that they use for marking. Males also have scent glands on their chest and wrists, the latter of which they use to mark their tail during stink fights (Kappeler 1990c). Individuals commonly mark the peripheries of their territories during inter-group interactions (Mertl-Millhollen 1988) and can even discriminate among individual odors (Mertl 1975, Palagi & Dapporto 2006).

METHODOLOGY:

Study Site:

This study was conducted at The Duke Lemur Center (DLC) in Durham, NC. The Duke Lemur Center houses multiple groups of ringtailed lemurs in several semi-free ranging enclosures that are surrounded by a mildly electrified fence. The two groups of ringtailed lemurs observed in this study lived in a 14.3-acre and 8.2-acre mixed pine hardwood forest. Several species of wild animals inhabit or visit the naturalistic

enclosures and act as potential predators and as competitors for food (Table 1). DLC is considered to be one of the four main sites for long-term ringtailed lemur research (Sauther *et al.* 1999). See Talyor (1986) and Wright (2008), for a complete description and history of the study site.

Time Frame:

The first field season took place between June 2007 and August 2007 and the second field season between June 2008 and August 2008. Observations were conducted between 7:00 and 16:00, five to six days a week. I controlled for the influence of time of day on behaviors by collecting the same amount of observations in the morning and in the afternoon for each focal animal.

Subjects:

In the summer of 2007, observations were conducted on seven ringtailed lemurs in an established species-typical social group (Table 2). In the summer of 2008, observations were conducted on another seven individuals from a different group of similar composition (Table 3) for a total sample size of 14. Similar sample sizes are common in other primate studies, including some conducted under completely natural conditions (Table 4). The adult animals have lived at DLC for at least three years and in most cases, all of their lives. Focal animals represented all gender, age, and reproductive classes that were present in each group.

The semi-free ranging animals at DLC are considered to be comparable both behaviorally and physically to wild lemurs (Sussman *pers. comm.*). In fact, a study on

ringtailed lemurs at St. Catherine's Island, another semi-captive facility in the United States, found that zoo animals released in these enclosures eventually resembled wild lemurs in terms of appearance and behavior (Keith-Lucas *et al.* 1999). In the past, six infants and two juveniles have died as the result of predation by the naturally existing predators that also inhabit the enclosures (Table 1). In response to these predators, DLC animals commonly partake in species typical mobbing and vocalization behaviors (Macedonia 1993, *pers. obs*.). The animal's diet was minimally supplemented in quantities that are 50% less than is required by the American Zoological Association for this species when it is maintained in zoos (Table 5). As a result, the animals forage on over 15 species of local flora that grow in the enclosures (Ganzhorn 1986) (Table 6), which takes up much of their feeding time. Furthermore, the average weight, and thus, net caloric intake of all adult lemurs are comparable to those of wild individuals (Koyama *et al.* 2007) (Table 7). This similarity suggests that there are comparable levels of feeding competition in these enclosures and in the wild.

Procedure:

Data Collection:

Data were collected using focal sampling of the 14 individuals previously noted. All focal individuals were observed in a random order for between 42 and 50 hours each (660 hours total). Focal behavior and group proximity scans of all visible group members were documented instantaneously at 5-minute intervals. Any occurrence of social behavior (Table 8) was documented continuously from the time of its onset to the

time of completion. Count data were documented opportunistically on the agonistic interactions that occurred between two or more non-focal animals.

I developed the following rubric for documenting behaviors. First, I classified a single social bout to be occurring if the behavior persisted with pauses of no more than 10 seconds. If the behavior ceased for more than 10 seconds, this indicated the end of that behavioral bout. Secondly, whenever an individual joined or left a social bout, subsequent interactions were considered to be a new bout. For example, if focal animal A was being groomed by B and then C moved into contact with A, this behavioral progression was scored as two distinct bout, the first of which involved grooming by B, and the second of which involved grooming by B and bodily contact with C.

When a social behavior occurred, I documented the identity of relevant individuals, the direction of each interaction, the type of behavior (Table 8), and the context in which the behavior occurred. The possible contexts were a) provisioned feeding (occasionally referred to as "feed"), b) naturalistic foraging (occasionally referred to as "forage"), c) rest, d) travel (directed locomotion with a beginning and end location), e) move (undirected movement), and f) alert. The context of social behaviors was determined based on the context category in which the animal was participating just prior to the initiation of a social behavior. For example, if two animals were foraging and one started to groom the other, this affiliative social behavior was considered to be taking place during a foraging context.

For all aggressive behaviors, I documented the behaviors that occurred just prior to the aggressive act. This measure is called the behavioral precedent to aggression. See

table 9 for an example data sheet and table 10 for supplemental information on the data sheet.

Coding Behaviors:

I coded all social behaviors using a combination of the following descriptive categories: *active* and/or *passive* and *affiliative* and/or *aggressive* (Table 8). For example, if focal animal A was grooming B, this bout was coded as *active affiliation*. Alternatively, if focal animal A was grooming B and was resting in contact with C, both interactions were treated as a single bout and were coded as *active passive affiliation*. However, if an active and passive behavior were occurring simultaneously in a behavioral bout between only two individuals, the active behavior took precedence. For example, if focal animal A was grooming B and B vocalized to A, this unit, which contained active (grooming) and passive (vocalization) elements, was coded as *active affiliation.* Submissive behaviors were coded as *passive aggression, submissive*. This coding system allowed me to conduct two main analyses. The first analysis was the total proportion of time that each focal individual spent in active and passive modes of behavior overall. In this analysis, single behavioral bouts involving three or more individuals that were coded as both active and passive in nature, were treated as active. Therefore, the active behavior took precedence because I was only interested in the overall nature of the behavioral bout. The second analysis that I conducted was to determine the proportion of time that each focal individual spent in active and passive behaviors with each of its group mates. In this analysis, if a single social bout include *active* social behavior with individual A and *passive* with individual B, that bout would

be classified as *active* when determining the time spent in social behavior with individual A, and *passive* when determining the time spent in social behavior with individual B. Therefore, *active* behaviors only took precedence when both an *active* and *passive* behaviors occurred simultaneously in a single unit between the same two individuals (as is described above). For example, if focal animal A chased B and B simultaneously vocalized, this bout, which contained passive (vocalization) and active (chase) elements, was classified as *active*.

I also coded agonistic behaviors by intensity level (Table 11). All passive agonism and submissive behaviors were assigned a number on a scale of 1-2 (Table 12). Active agonistic interactions were assigned a number on a scale of 3-7 (Table 12). Those behaviors that were assigned a number between 1-4 were considered to be low intensity aggression and those that were assigned a number between 5-7 were considered high intensity aggression (Table 12). The intensities were assigned based on the presumed likelihood of each behavior causing physical harm; these classifications are similar to the categories used by Arnold and Whiten (2001). For each individual, I determined the overall rate per hour of intense vs. mild agonistic behaviors in all contexts.

Classification of Feeding Contexts:

There were two feeding contexts experienced by the ringtailed lemurs in this study, which were termed as the "provisioned feeding" and the "naturalistic foraging" contexts. In the provisioned feeding context, the lemurs fed on primate chow, which was classified as a highly valuable food source because it is designed to be nutritionally complete for primate species (Mowry & Campbell 1991). The provisioned feeding context was also

classified as a clumped resource. A proximity analysis conducted in chapter 2 (Sbeglia 2009) confirmed that the individuals in both groups maintained significantly larger inter-individual distances in the naturalistic foraging context as compared to the provisioned feeding context. Lastly, the provisioned feeding context was also classified as containing a limited food resource because the chow was provisioned at quantities that are over 50% less than is required by the American Zoological Association for this species (Table 5) and because both groups of ringtailed lemurs consistently ate the entire ration (69.4g/individual/day) of chow and continued to search for more after it ran out. In the naturalistic foraging context, the lemurs fed on fruits, leaves, bugs, and flowers. This context was classified as containing less valuable food resources that were more plentiful and dispersed through space and time.

Analysis:

Measures of Resource Competition:

The degree of resource competition experienced by the social groups was measured in two ways. The first is the amount of agonism that occurs in feeding contexts (Pruetz 2009). This value was determined as an average rate of active and passive agonism per individual per hour in each of the two food-oriented contexts. The second measurement is the encounter rate with food, with lower encounter rates suggesting heightened competition (Sterck *et al*. 1997). This value was calculated using the instantaneous data by determining the proportion of 5-minute intervals during which the focal animal was observed to be feeding. This analysis was done separately for the feeding and the foraging contexts.

Coalition Formation:

Although not done in this study, this data set can be used to gain information on coalition formation. Coalitions can be considered to occur when more than one individual was simultaneously involved as an aggressor in an agonistic act. However, although this classification operationally defines a coalition, it does not necessarily imply that individuals are purposefully working towards a collective goal. Coalitionary support is expected to aid in the establishment and maintenance of stable and linear dominance hierarchies (Sterck *et al.* 1997). Frequent coalitions among relatives are predicted to co-occur with decided agonistic dominance relationships and result in a nepotistic dominance hierarchy (Sterck *et al.* 1997).

Formal Submission:

Again, although not done in this study, this data set can also be used to gain information on formal submission. Formal submission indicates subordinant status (de Waal 1989) and is considered to occur when 1) a suite of vocal and behavioral signals are consistently used by subordinant animals towards dominant individuals, 2) the vocal and behavioral signals follow a high degree of linearity, 3) there is a predictive relationship between the submission hierarchy and other agonistic hierarchies, 4) they are directed only at conspecifics and members of the same group, 5) the signals are used with spontaneity, and 6) with specificity (Lu *et al.* 2008). Submissive behaviors in ringtailed lemurs include jumping away, fleeing, squealing, and yip/spat calls (Jolly 1966, Taylor & Sussman 1985, Macedonia 1993, Sauther *et al.* 1999). Submissive animals are also displaced by dominant individuals even in the absence of obvious agonism.

Proximity:

Proximity is the inter-individual distance at 5-minute intervals that each focal animal is from other group members. With these data I determined the average inter-individual distance between each focal animal and all other group members and the average number of individuals within 10 meters of the focal animal.

Reconciliation:

The relationship between previous aggression and social behavior patterns was analyzed using a framework similar to that of the reconciliation hypothesis. The reconciliation hypothesis states that aggression influences affiliation patterns by promoting friendly contact between previous combatants soon after the cessation of a fight (de Waal & van Roosmalen 1979). Reconciliation is believed to function to repair relationships that were damaged by aggression (de Waal & van Roosmalen 1979), to reduce future aggression (Castles & Whiten 1998), reduce the stress of previous combatants (Katsukake & Castles 2001) and restore tolerance in the presence of food (Aureli *et al.* 2002). Reconciliation has thus become accepted as a behavioral mechanism that preserves the cohesion of social groups by reducing the negative impacts of conflict (Silk 2002). An implication of this hypothesis is that affiliative reconciliatory behaviors are repair mechanisms to counter the unavoidable conflict that is expected to occur in a social group (Fuentes 2004, Sussman *et al*. 2005). Researchers have documented reconciliation in many species of primates (Aureli & de Waal 2000) and other social mammals (Schino 1998, domestic goats, *Capra aegagrus*; Wahaj *et al.* 2001, spotted hyenas, *Crocuta crocuta*).

In addition to serving a reconciliation function, post-conflict conciliatory behavior has also been found to occur between an uninvolved individual and the victim of an aggressive interaction. This triadic post-conflict affiliation has been termed "consolation" and is thought to be an effective conflict management mechanism because it may curtail ongoing aggression (Petit & Thierry 1994). Furthermore, because the consoling third party may be the kin of the opponent (Judge 1991, Call *et al.* 2002, Wittig *et al.* 2007), "consolation" can also restore affiliation across genetic lines. Judge and Mullen (2005) have further argued that quadratic reconciliation, where bystanders not involved in a fight affiliate with each other in the post-conflict period, can also function to control conflict and restore relationships through the group-wide reduction of tension. Arnold and Whiten (2001) and Fuentes *et al.* (2002) did not find evidence of this behavior in wild chimpanzees, *Pan troglodytes schweinfurthii,* which lead them to suggest that "consolation" is not a post-conflict behavior of this species in their natural habitat. Although they are often used as such in the literature (Silk 2002), the terms "reconciliation" and "consolation" do not necessarily indicate purposeful behaviors intended to end conflict. In this study, reconciliation and consolation only referred to the operational definition of the terms (i.e. heightened affiliation after conflict) and did not imply emotional outcomes.

"Reconciliation" traditionally has been studied by comparing the affiliation that occurs between previous combatants, in a specified post-conflict time period, with the affiliation that occurs between these individuals during an identical time interval (de Waal & van Roosmalen 1979) and at a similar inter-individual distance (Call 1999) the next day. For example, if a post conflict period occurs at 10:00 while the individuals are

4 meters away from one another, the matched control period would occur at around 10:00 the next day when the individuals are at a similar inter-individual distance. This procedure is called the Post Conflict-Matched Control (PC-MC) method. Most studies using this method specify a 10-minute post conflict time interval because that is when most post-conflict affiliations have been found to occur (Kutsukake & Castles 2004, Arnold & Whiten 2001).

The PC-MC method has been primarily used in captivity and is not entirely appropriate for semi-captive or wild studies due to the subjects increased ability for movement (Arnold & Whiten 2001, Kutsukake & Castles 2004). Therefore, Kutsukake and Castles (2004) refined the method by choosing the MC time interval, a posteriori, from the focal animal sampling data. The MC period was matched with the activity of the focal animal during the PC period and was initiated when the focal animal was within 10 meters from the previous combatant. Because even these conditions are difficult to meet in semi-captive and wild conditions, Arnold & Whiten (2001) relaxed the criteria to allow up to 23 days to pass between the PC and MC time intervals.

An assumption of the PC-MC method is that the MC time period accurately indicates the relationship that would exist between two individuals in the absence of a fight. This assumption is most likely unrealistic because matched-control observations do not necessarily reflect the baseline affiliation of individuals in the absence of a fight (Kappeler & van Schaik 1992, Silk 1997). Furthermore, this method does not take into account the variation in the frequency and type of social interactions that exist through time. These oversights can result in erroneous conclusions about the patterns of "reconciliation" within social groups because the documentation process of the

occurrences of this behavior is highly subject to chance events. As a result, Kappeler & van Schaik (1992) proposed the baseline method, which involves conducting several observations of affiliative behavior throughout the study period to get a baseline level of affiliation to which post-conflict behavior can be compared. I used a similar method in this study except that I compared post-conflict behavior to many random time periods selected post-hoc from the entire data set.

In this study, "reconciliation" was considered to occur when previous opponents made affiliative contact, either active or passive, in the post-conflict time period significantly sooner than at multiple random 10-minute time intervals throughout all observation days. A 10-minute post-conflict interval was initiated in a post-hoc fashion immediately after the secession of an active aggressive interaction. A requirement for all qualifying post-conflict time intervals was that they do not contain an active aggressive interaction. To determine if affiliative behavior occurred sooner in the post-conflict time period than at random time periods, thus indicating "reconciliation", 40 random time intervals were extracted from each focal individual's observation days. The latency to affiliate with the previous opponent in the post conflict period and in each random time periods was calculated. I also calculated the latency of third party affiliation (i.e. "consolation") in the post-conflict time period and the latency of affiliation with all group members in the random time periods. A similar method was used to determine if there was a relationship between previous agonism and future agonism. In this analysis, the latency of an aggressive interaction with a previous combatant was calculated for each post-conflict time period and each random time period. Active agonism was allowed to

Several factors were analyzed as potential predictors of heightened affiliation

and/or agonism between previous combatants and third party individuals after a fight. This was done by separating conflicts, and their accompanying post-conflict period, into three categories based on: 1) its intensity, 2) the degree of relatedness of the combatants, 3) overall rates of affiliation between previous combatants and 4) overall rates of agonism between previous combatants.

Behavioral Precedent to Conflict:

For this study, behavioral precedent refers to the behaviors of all involved individuals that immediately precede an aggressive interaction. This term does not imply causation. Two non-mutually exclusive analyses were conducted. The first analysis involved coding behaviors as either food-oriented or non-food-oriented and the second analysis involved coding behaviors as either close proximity movement or other. The purpose of these analyses were to determine the proportion of aggressive interactions that were preceded by each category of behavior.

Kinship:

Degrees of relatedness were measured using the coefficient of relatedness, r, which were determined based on the known pedigree relationships between individuals (Table 1, Table 2). Individuals were categorized as having a coefficient of relatedness of $r \geq 0.5$, $0.5 < r > 0.0$, or $r = 0.0$.

Dominance Hierarchy:

Interaction patterns among group mates, is a major aspect of social organization,

which is characterized as being egalitarian, despotic, or somewhere in between (van

Schaik 1989). The degree to which interactions are egalitarian or despotic is measured

by the linearity of relationships within a hierarchy (de Vries 1995). The linearity of

social interactions measures the degree of transitivity among individuals. A completely

transitive, and thus linear set of interactions exist when A is dominant over B and A and

B are both dominant over C, etc. (de Vries 1995). If social interactions occur in a linear

manner, the social group is said to have dominance hierarchy and individuals can be

ranked according to their agonistic and submissive interactions. In the Socioecological

model, the characteristics of the dominance hierarchy are primary variables used to

classify the organization of primate social group s. The social interaction patterns in this

study population were determined by creating matrices containing frequency information

of the winner and loser of all decided agonistic interactions. Decided interactions are

conflicts in which one animal exhibits a submissive behavior while the other animal

either exhibits or does not exhibit an agonistic behavior (Pereira *et al.* 1990, Nakamicki

& Koyama 1997). Those conflicts in which one animal exhibits an agonistic behavior

and the other exhibits just an agonistic behavior or both an agonistic and submissive

behavior are not considered to be decided agonistic interactions (Nakamicki & Koyama

1997).

The values in each cell were a combination of each dyad's interactions during each

of their focal observation days (approximately 100 hours of observation for each dyad).

Because high and low intensity agonism exhibited very different patterns in this study

population in previous analyses (Chapter 2, Sbeglia 2009), separate matrices were created

for high and low intensity behaviors for all analyses (Table 9). Low intensity behaviors

included submissive vocalizations, which unlike other agonistic behaviors, are directed away from subordinant individuals and towards dominant individuals. Therefore, I transposed the direction of all submissive behaviors for these analyses. For non-focal animals, matrix values were determined based on that individual's interactions with a focal animal during that focal animal's observation days. The interaction patterns of two non-focal animals were determined using approximately 200 hours of count data that was opportunistically collected during focal observations. This method was only used for active agonistic interactions because passive agonism (Table 8) is often so subtle that it was likely that the interaction patterns indicated by those data would be inaccurate. Therefore, for the low intensity agonism matrices, the interaction patterns of non-focal dyads could not be determined and were treated as having an unknown relationship. Males and females were placed in the same matrix but their interaction patterns were interpreted both independently, as suggested by Jolly (1966), and together.

TABLES:

Table 1: Potential predators of ringtailed lemurs in captivity and in the wild

Potential North American Predators	Ecological Equivalent in Madagascar (the categories, not necessarily individual species, are comparable)
Raptors:	
red-tailed hawk[1] (*Buteo jamaicensis*) red-shouldered hawk[1] (*Buteo lineatus*) great-horned owl[1] (*Bubo viginianus*)	Madagascar harrier hawk[2,5] (*Polyboroides radiatus*) Madagascar buzzard [2,5] (*Buteo brachypterus*) black kite[5] (*Milvus migrans*)
Carnivores:	
gray fox[1] (*Urocyon cineroagenteus*) raccoon[1] (*Procyon locor*) weasel[1] (*Mustela sp.*)	fossa[3] (*Cryptoprocta ferox*) domestic dog [4] (*Canis lupus familiaris*) domestic cat[5] (*Felis catus*)
Venomous snakes:	
copperhead[1] (*Agkistrodon contortrix*) cottonmouth[1] (*Agkistrodon piscivorus*)	NA
Non-venomous Snakes:	
black rat snake[1] (*Elaphe obsolete*)	Madagascar boa constrictor [3] (*Boa manditra*)

[1]Macedonia (1993), [2] Sauther (1989), [3]Karpanty & Wright (2007), [4]Gould & Sauther (2007), [5]Jolly *et al.* (2006)

Table 2: Composition of social group 1

Name	Gender	Age	Classification	Relatedness
Fern	F	3 mo	Natal infant	Offspring of Cleis and Alexander, half sib of Persephone and Dory, niece of Alena, Tellus, and Niciea
Persephone*	F	2 yrs	Natal juvenile	Offspring of Cleis & Aracus, full sib of Ivy, half sib of Dory, half aunt and half sib of Niciea, Tellus, Alena, and Alex
Alena	F	2 yrs	Natal juvenile	Offspring of Dory & Aracus, grand daughter of Cleis,, full sib to Alex, Niciea, and Tellus, half sib to Berisidies, aunt of Fern, half sib and half nephew of Ivy and Persephone
Niciea*	F	3 yrs	Natal sub-adult	Offspring of Dory & Aracus, grand daughter of Cleis, full sib of Alena, Tellus, and Alexander, aunt to Fern, half sib and half nephew of Ivy and Persephone
Tellus	F	3 yrs	Natal sub-adult	Offspring of Dory & Aracus, grand daughter of Cleis, full sib of Alena, Niciea, and Alexander, aunt to Fern, half sib and half nephew of Ivy and Persephone
Dory*	F	18 yrs	Natal adult	Offspring of Cleis and unrelated male, mother of Tellus, Niciea, Alexander and Alena, half sib of Persephone and Fern, aunt of Berisidies
Cleis*	F	22 yrs	Founder, lactating adult	Offspring of Lethe and Pegasis, mother of Dory, Persephone, Ivy, and Fern, grandmother to Berisidies
Alexander*	M	2 yrs	Natal juvenile, pre-dispersal age	Offspring of Dory & Aracus, grand son of Cleis, father of Fern, full sib of Alena, Niciea, and Tellus
Ivy	M	3 yrs	Natal sub-adult of dispersal age	Offspring of Cleis & Aracus, full sib of Persephone, half sib of Dory, half sib and half uncle to Niciea, Tellus, Alena, and Alex
Berisidies*	M	3 yrs	Natal sub-adult of dispersal age	Offspring of Sosiphanes & Aracus, half sib and cousin of Niciea, Tellus, Alena, and Alex, nephew of Dory, grandson of Cleis, half nephew and half sib of Persephone and Ivy
Fritz	M	5 yrs	Non-natal adult	Half sib of Cap N' Lee
Cap N' Lee*	M	7 yrs	Non-natal adult	Half sib of Fritz

*Focal animals (no data were collected on interactions with infants, <1yr)

Table 3: Composition of social group 2

Name	Gender	Age	Classification	Relatedness
Nebe*	F	5 yrs	Natal adult	Offspring of Hector and Katina, mother of Herodotous, half sib of Dorius, half aunt of Justine and half aunt of Cebes
Dorius*	F	12 yrs	Natal adult	Offspring of Gelon and Katina, mother of Justine and Cebes, half sib of Nebe, half aunt of Hero
Sophia*	F	4 yrs	Natal sub-adult	Offspring of Artemesia and Brennus, half sib of Justine
Justine*	F	3 yrs	Natal sub-adult	Offspring of Dorius and Brennus, half sib of Sophia, half niece of Nebe, half cousin of Herodotus
Chandler*	M	7 yrs	Non-natal adult	Offspring of unrelated individuals, father of Cebes and Herodotous
Cebes*	M	2 yrs	Natal juvenile, pre-dispersal age	Offspring of Dorius and Chandler, half sib and half cousin of Herodotous, half sib of Justine, half nephew of Nebe
Herodotus*	M	2 yrs	Natal juvenile, pre-dispersal age	Offspring of Nebe and Chandler, half sib and half cousin of Cebes, half nephew of Dorieus

*Focal animals

Table 4: Sample sizes of various primate studies in captivity and in the wild

Author(s)	Year	Species	Subject	# of focal indiv.	# hrs of Observation
Gould*	1996	ringtailed lemurs	Affiliative relationships	10	1102
Keith-Lucas *et. al.*	1999	ringtailed lemurs	Changes in behavior after release	6	Not provided
Arnold & Barton	2001	speckled leaf monkeys	Reconciliation/Post conflict behavior	12	165
Sussman *et al.* *	2003	ringtailed lemurs	Aggression and affiliation frequencies	4	40
Wittig & Boesch*	2003	chimpanzees	Feeding competition	14	1028
Mallavarapu *et al.*	2006	gorillas	Reconciliation/Post conflict behavior	13	223+
Parga	2006	ringtailed lemurs	Male mate choice	11	Not provided
Wittig *et al.*	2007	baboons	Kin mediated reconciliation	13	Not provided
Palagi *et al.* *	2008	Verreauxi's Sifaka	Reconciliation/Post conflict behavior	16	640

*Studies conducted in the wild

Table 5: Amount of provisioned food

	Chow per indiv. per wk(g)	% of provisioned diet	Fruit & veg. per indiv. per wk(g)	% of provisioned diet	Total food per indv. per wk(g)
Duke Lemur Center[1]	486	56.71%	371	43.29%	857
St. Louis Zoo[2]	588	32%	1260	68%	1848

[1] Duke Lemur Center (2007), [2] St. Louis Zoo (2007)

Table 6: Plant species and plant parts in the diet of *Lemur catta* at Duke Lemur Center. Adapted from Ganzhorn (1986) (N = 402)

Species	ML	YL	PE/PU	LB	Bark	FL/FR	Other	Total
Liquidambar styraciflua	1.7	16.4	3.5	0	1.2	—	0.8	23.6
Pinus taeda	14.9	1.5	0	0	0.5	0.5	2.0	19.4
Viburnum rafinesquianum	0	5.2	0	0	0.5	2.2	1.7	9.6
Lonicera japonica	0.5	0	0	0	0.5	6.0	0.3	7.3
Poaceae spp.	1.0	5.2	0	0	0	0	0	6.2
Diospyros virginiana	0.8	3.0	0	0.3	0.8	0	0	4.9
Quercus spp.	0.8	2.7	0	0	0.3	0	1.0	4.8
Juniperus virginiana	0.8	0	0	0	3.5	0	0	4.3
Cercis canadensis	0.3	2.5	0	0	0	0	0.8	3.6
Acer rubrum	1.0	1.5	0	0	0.3	0	0	2.8
Rhus radicans	2.0	0	0	0	0	0.3	0	2.3
Fraxinus americana	0	0.8	0.5	0	0	0	0	1.3
Hypericum hypericoides	0	1.0	0	0	0	0	0	1.0
Liriodendron tulipifera	0	0.5	0	0	0	0	0.5	1.0
Malus coronaria	1.0	0	0	0	0	0	0	1.0
Other (each < 1%)	0.5	2.2	0	0.3	0.3	0	2.0	5.3
Unidentified								2.0
Total	25.3	42.5	4.0	0.6	7.9	9.0	9.1	

"ML, mature leaves (whole or blade only); YL, young leaves; PE/PU, petioles or pulvini; LB, leaf buds; FL/FR, flowers or fruits; —, not available.

Table 7: Average weights of ringtailed lemurs

	Berenty Reserve[1]	Duke Lemur Center[2]	St Louis Zoo[3]	Miami MetroZoo[4]
	Wild	**Semi-free Ranging**	**Captive**	
Adult Female	2.27 kg	2.32 kg	3.52kg	2.73kg
Adult Male	2.22 kg	2.36 kg	2.7kg	4.1kg

[1] Koyama, *et. al* (2007), [2] Duke Lemur Center (2007), [3] St. Louis Zoo (2007), [4] Miami MetroZoo (2007)

Table 8: Categorization of behaviors

Active Affiliation:		Passive Affiliation:
Groom		Rest in Contact
Mutual Groom		Drink in contact
Play		Forage in contact
		Feed in contact
		Self groom in contact
		Alert in contact
		Contact Voc. (meow*, moan*, wail*)
		Sniffing others
Active Agonism:		**Passive Agonism:**
Chase	Touch	Displace
Chase threat	Grab	Chutter/Deep spat*
Bite	Push	Plosive Bark*
Lunge	Food take	
Lunge threat	Wrestle	
Hit	Stink fight[1]	
Mouth to face threat		
Passive Aggression, Submissive:		**Predator/Alert Vocalization:**
Yip/Spat call*		Bark/yap*
Flee and Squeal*		Gulp*
		Shriek*
Unknown:		
Stink fight[1]		
Food share/take[2]		
Cackle*[3]		

*Terms taken from Macedonia (1993)

[1]A stink fight can represent both an aggressive and a sexual interaction depending on the individual to whom the behavior is directed. Therefore, a stink fight behavior is considered to be *active aggression* when it is directed at a male and *unknown* when directed at a female.

[2]It is impossible to tell whether individuals are actively sharing food or behaving submissively.

[3] This behavior is thought to be a defensive vocalization indicating a willingness to become aggressive if pressed (Macedonia 1993). Therefore, it is unclear as to whether it is *submissive* or *agonistic*.

Table 9: Example Data Sheet (match up pages 185-187 horizontally)
Focal: Nebe

Category*	Inten-Sity*	Score*	Date	5 min	Precedent Performer	Precedent Receiver	Cont-ext	Time
			1-Jul	x			Fr	14:20:00
pass, agg	M	2	1-Jul		forage	forage	Fr	14:20:19
			1-Jul				Fr	14:20:20
act, agg	I	5	1-Jul		rest	move	Fr	14:23:23
			1-Jul				Fr	14:23:24
			1-Jul	x			Fr	14:25:00
pass, agg, sbmsv	M	1	1-Jul		travel	feed	T	14:28:54
			1-Jul				T	14:28:55
			1-Jul	x			T	14:30:00
pass, aff			1-Jul				T	14:31:05
pass, aff			1-Jul				T	14:32:27
			1-Jul	x			T	14:35:00
pass, aff			1-Jul				M	14:38:43
pass, aff			1-Jul				M	14:38:49
pass, aff			1-Jul				M	14:39:41
			1-Jul	x			M	14:40:00
pass, aff			1-Jul				M	14:40:23
pass, aff			1-Jul				M	14:41:47
			1-Jul	x			A	14:45:00
			1-Jul	x			T	14:50:00
			1-Jul	x			T	14:55:00
pass, aff			1-Jul				T	14:57:55
			1-Jul				T	14:58:17
			1-Jul	x			T	15:00:00
			1-Jul	x			T	15:05:00
			1-Jul	x			T	15:10:00
			1-Jul	x			M	15:15:00
pass, aff			1-Jul				M	15:19:46
			1-Jul	x			M	15:20:00
pass, aff			1-Jul				T	15:20:41
			1-Jul				T	15:20:42
act, aff			1-Jul				T	15:23:22
			1-Jul				T	15:23:24
pass, aff			1-Jul	x			T	15:25:00
			1-Jul	x			T	15:30:00
pass, aff			1-Jul				T	15:32:46
act, aff			1-Jul				T	15:32:52
pass, aff			1-Jul				T	15:33:08
			1-Jul				T	15:33:12
act, aff			1-Jul				T	15:33:28

*Column information determined post-data collection

Behavior	End Time	With	Direction	Duration	Dist (m)	1	2	3	4
f	ND				0.50	N			
d+	ND	n -> s	to	0:00:01					
d-	14:20:20								
lunge+	ND	s -> h	away	0:00:01					
lunge-	14:23:24								
out of sight	ND								
yip+	ND	s -> n	away	0:00:01					
yip-	14:28:55								
r	ND				1.00	N	J		
meow	ND								
sm	ND								
r	ND				0.05	D			
meow	ND								
meow	ND								
meow	ND								
m	ND				2.00	D			
sm	ND								
sm	ND								
alert	ND				5.00	N			
r	ND				2.00	D			
r	ND				0.05	D			
n mc rc+	ND	N		0:00:22					
rc-	14:58:17								
r	ND				0.20	D			
r	ND				0.10	Ch			
t	ND				2.50	D			
r	ND				4.00	N	J		
meow	ND								
r	ND				1.00	N			
smell+	ND	S -> j	away	0:00:01					
smell-	15:20:42								
j mc mg+	ND	S <-> J	to, away	0:00:02					
mg-, c-	15:23:24								
drink	ND				2.50	Ch			
sg	ND				2.50	Ce	D		
mc rc+	ND	D		0:00:06					
rc-; g+	15:32:52			0:00:16					
g-; j mc rc+, rc+	15:33:08	D, j		0:00:04					
rc-	15:33:12								
ce Mc Mg+	ND	s <-> ce	to, away	0:00:47					

Dist (m)	1	2	3	4	Dist (m)	1	2	3	4	Dist (m)	1	2	3	4
1.50	H				5.00	Ch				7.50	J			
5.00	N													
8.00	H	Ce			15.00	Ch								
4.50	N				18.00	Ch	J	Ce						
10.00	N	J			20.00	?								
0.50	Ce				1.00	N				2.00	J			
0.20	D				18.00	N								
3.00	N													
8.00	D													
2.00	H	D			4.00	Ch				6.00	J			
10.00	N				12.00	H								
3.00	H				8.00	J				8.50	N			

Table 10: Supplemental information for example data sheet

Acronym	Meaning
Mg	Mutual groom between the focal animal and a conspecific
Mgc	Mutual groom while in contact with another individual
G	Groom
Gc	Groom while in contact with another individual
Sg	Self groom
Sgc	Self groom in contact with another individual
Rc	Rest in contact
R	Rest
Mc	When the focal animal moves into contact with a conspecific
XX Mc	The *XX* is replaced with the acronym for the specific individual that moved into contact with the focal animal
T	Travel
sm	Scent mark
om	Overmark
M	Move
Sf	Stink fight
fs	food share
ft	Food take
wr	When the wrists are used for scent marking
ag	When anogenital glands are used for scent marking
Fr	Forage
F	Feed
R	Rest
J	Justine
Ce	Cebes
N	Nebe
Ch	Chandler
D	Dorieus
S	Sophia
H	Herodotus

Table 11: Behaviors that constitute high and low intensity agonism

	High Intensity	Low Intensity
Active Aggression	Stink fight Bite Hit Lunge Wrestle Chase	Chase threat Push Lunge threat Grab Food Take Touch Mouth to face threat*
Passive Aggression	None	Cackle/Deep spat* Chutter* Yip/Spat call* Displace Plosive bark* Squeal*

*Terms taken from Macedonia (1993)

Table 12: Categorization of agonism by intensity

Behavior Category	Intensity Score	Intensity Level
Submissive and agonistic vocalizations	1	Low
Displace/supplant	2	Low
Mouth to face threat	3	Low
Threats of high intensity agonism (ex. chase threat)	4	Low
Chase, lunge, stink fight*	5	High
Unidirectional contact (ex. push, grab, hit)	6	High
Uni- or multidirectional fighting	7	High

*Between males only

LITERATURE CITED:

Arnold, K. & Barton, R. A. (2001) Postconflict behavior of spectacled leaf monkeys (*Trachypithecus obscurus*). *International Journal of Primatology* 22(2): 244-266.

Arnold, K. & Whiten, A. (2001) Post-conflict behaviour of wild chimpanzees (*Pan troglodytes schweinfurthii*) in Budongo Forest, Uganda. *Behaviour* 138: 649–690.

Aureli, F., Cords, M., & van Schaik, C. P. (2002) Conflict resolution following aggression in gregarious animals: a predictive framework. *Animal Behaviour* 64: 325–343.

Aureli, F. & de Waal, F. B. M. (2000). *Natural Conflict Resolution*. Berkley: University of California Press.

Call, J. (1999). The effect of inter-opponent distance on the occurrence of reconciliation in stumptail (*Macaca arctoides*) and rhesus macaques (*Macaca mulatta*). *Primates* 40: 515-523.

Call, J., Aureli, F. & de Waal, F. B. M. (2002) Postconflict third-party affiliation in stumptailed macaques. *Animal Behaviour* 63: 209– 216.

Castles, D. L. & Whiten, A. (1998) Post-convict behaviour of wild olive baboons. I. reconciliation, redirection and consolation. *Ethology* 104: 126–147.

Duke Lemur Center (2007) Documents provided by staff. Durham, NC.

Ehart, E. M. & Overdorff, J. D. (2008) Rates of agonism by diurnal lemuroids: implications for female social relationships. *International Journal of Primatology* 29: 1227-1247.

Fuentes, A. (2004) Revisiting conflict resolution: Is there a role for emphasizing negotiation and cooperation instead of conflict and reconciliation? In: *The Origins and Nature of Sociality* (eds. R. W. Sussman and A. R. Chapman) New York: Aldine de Gruyer, pp 215-236.

Fuentes, A., Malone, N., Sanz, C., Matheson, M., Vaughan, L. (2002) Conflict and post-conflict behavior in a small group of chimpanzees. *Primates* 43: 223–236.

Ganzhorn, J. U. (1986) Feeding behavior of *Lemur catta* and *Lemur fulvus*. *International Journal of Primatology* 7(1): 17-30.

Gould, L. (1990) The social development of free-ranging infant *Lemur catta* at Berenty reserve, Madagascar. *International Journal of Primatology* 11: 297-318.

Gould, L. (1992) Alloparental care in free-ranging *Lemur catta* at Berenty Reserve, Madagascar. *Folio Primatologica* 58: 72-83.

Gould, L. (1994) Patterns of affiliative behavior in adult male ringtailed lemurs (*Lemur catta*) at the Beza Mahafaly Reserve, Madagascar. Ph.D. thesis, Washington University, St. Louis, MO.

Gould, L. (1996) Male-female affiliative relationships in naturally occurring ringtailed lemurs (*Lemur catta)* at the Beza-Mahafaly Reserve, Madagascar. *American Journal of Primatology* 39: 63-78.

Gould, L. & Sauther, M. L. (2007) Anti-predator strategies in a diurnal prosimian, the ring-tailed lemur (*Lemur catta*), at the Beza Mahafaly Special Reserve, Madagascar. In: *Developments in Primatology: Progress and Perspectives part 3* (eds. S. L. Gursky and K. A. I. Nekaris). New York and Oxford: Oxford University Press.

Gould, L. Sussman, R. W., & Sauther, M. L. (1999) Natural disasters and primate populations: the effects of a two-year drought on a naturally occurring population of ringtailed lemurs (*Lemur catta*) in southwestern Madagascar. *International Journal of Primatology* 20: 69-84.

Hood, L. C. & Jolly, A. (1995) Troop fission in female *Lemur catta* at Berenty Reserve, Madagascar. *International Journal of Primatology* 16; 997-1015.

Judge, P. G. (1991) Dyadic and triadic reconciliation in pigtail macaques (*Macaca nemestrina*). *American Journal of Primatology* 23: 225–237.

Judge, P. G. & Mullen (2005) Quadratic postconflict affiliation among bystanders in a hamadryas baboon group. *Animal Behaviour* 69: 1345-1355.

Jolly, A. (1966) *Lemur Behavior: A Madagascar Field Study*. Chicago and London: The University of Chicago Press.

Jolly, A., Sussman, R. W., Koyama, N., & Rasamimanana, H. (2006) *Ringtailed Lemur Biology: Lemur catta in Madagascar*. Springer.

Kappeler, P. M. (1990a) The evolution of sexual dimorphism in prosimian primates. *American Journal of Primatology* 21:201-214.

Kappeler, P. M. (1990b) Female dominance in Lemur catta: more than just female feeding priority? *Folia Primatologica* 55: 92-95.

Kappeler, P. M. (1990c) Social status and scent marking behavior in Lemur catta. *Animal Behaviour* 40(4): 774-776.

Kappeler, P. M. (1993) Reconciliation and post-conflict behavior in ringtailed lemurs, *Lemur catta*, and red fronted lemurs, *Eulemur fulvus rufus*. *Animal Behavior* 45: 901-915.

Kappeler, R. M. & van Schaik, C. P. (1992) Methodological and evolutionary aspects of reconciliation among primates. *Ethology,* 92:51-69.

Karpanty, S. & Wright, P. C. (2007) Predation on lemurs in the rainforests of Madagascar by multiple predator species: Observations and experiments. In: *Developments in Primatology: Progress and Perspectives part 2* (eds. S. L. Gursky and K. A. I. Nekaris). New York: Springer.

Keith-Lucas, T., White, F. J., Keith-Lucas, L. & Vick, L. G. (1999) Changes in behavior in free-ranging *Lemur catta* following release in a natural habitat. *International Journal of Primatology* 47: 15-28.

Koyama, N., Aimi, M., Kawamoto, Y., Harai, H., Go, Y., Ichino, C. & Takahata, Y. (2007) Body mass of wild ringtailed lemurs in Berenty Reserve, Madagascar, with reference to tick infestation: a preliminary analysis. *Primates* 49(1): 9-15.

Kutsukake, N. & Castles, D. L. (2001) Reconciliation and variation in post-conflict stress in Japanese macaques (*Macaca fuscata fuscata*): Testing the integrated hypothesis. *Animal Cognition* 4: 259–268.

Kutsukake, N. & Castles, D., L. (2004) Reconciliation and post-conflict third-party affiliation among wild chimpanzees in the Mahale Mountains, Tanzania. *Primates* 45: 157-165.

Lu, A., Koenig, A., & Borries, C. (2008) Formal submission, tolerance and socioecological models: a test with female Hanuman langurs. *Animal Behaviour* 76: 415-428.

Macedonia, J. M. (1993) Vocal repertoire of the ringtailed lemur (*Lemur catta*). *Folia Primatologica* 61: 186-217.

Mallavarapu, S., Stoinski, T.S., Bloomsmish, M. A. & Maple, T. L. (2006) Postconflict behavior in captive western lowland gorillas (*Gorilla gorilla gorilla*). *American Journal of Primatology* 68: 789-801.

Mertl, A. S. (1975) Discrimination of individuals by scent in a primate. *Behavioral Biology* 14(4): 505-509.

Mertl-Millhollen, A. S. (1988) Olfactory demarcation of territorial but not home range boundaries by *Lemur catta*. *Folia Primatologica* 50: 175-187.

Miami MetroZoo (2007) Documents provided by staff. Miami, FL.

Mowry, C. B. & Campbell, J. L. (2001) Nutrition. In: *Ring-tailed Lemur (Lemur catta) Husbandry Manual*. American Association of Zoos and Aquariums.

Nakamichi, M. & Koyama, N. (1997) Social relationships among ringtailed lemurs (*Lemur catta*) in two free-ranging troops at Berenty Reserve, Madagascar. *American Journal of Primatology* 18(1): 73-93.

Palagi, E. & Dapporto, L. (2006) Beyond odor discrimination: demonstrating individual recognition by scent in *Lemur catta*. *Chemical Senses* 31: 437-443.

Palagi, E. Antonacci, D., & Norscia, I. (2008) Peacemaking on treetops: first evidence of reconciliation from a wild prosimian (*Propithecus verreauxi*). *Animal Behaviour* 76: 737-747.

Palagi, E., Paoli, T., & Tarli, S. B. (2005) Aggression and reconciliation in two captive groups of *Lemur catta*. *International Journal of Primatology* 26(2): 279-294.

Parga, J. (2006). Male mate choice in *Lemur catta*. *International Journal of Primatology* 27(1): 107-131.

Pereira, M. E. (1995) Development and social dominance among group-living primates. *American Journal of Primatology* 37: 143-175.

Pereira, M. E. & Kappeler, P. M. (1997) Divergent systems of agonistic relationships in lemurid primates. *Behaviour*. 134: 225-274.

Pereira, M. E., Kaufman, R., Kappeler, P. M., & Overdorff, D. J. (1990) Female dominance does not characterize all of the lemuridae. *Folia Primatologica* 55: 95-103.

Petit, O. & Thierry, B. (1994) Aggressive and peaceful interventions in conflicts in Tonkean macaques. *Animal Behaviour* 48: 1427– 1436.

Pruetz, J. D. E. (2009) *The Socioecology of Adult Female Patas Monkeys and Vervets in Kenya.* New Jersey: Pearson Education Inc.

Rasamimana, H. R. & Rafidinarivo, E. (1993) Feeding behavior of *Lemur catta* females in relation to their physical state. In: *Lemur Social Systems and their Ecological Basis* (eds. P. M. Kappeler and J. U. Ganzhorn). New York: Plenum Press, pp123-133.

Rolland, N. & Roeder, J. J. (2000) Do ring tailed lemurs (*Lemur catta*) reconcile in the hour after post-conflict: A pilot study. *Primates* 41(2): 223-227.

Sauther, M. (1989) Antipredator behavior in troops of free-ranging *Lemur catta* at Beza Mahafaly special reserve, Madagascar. *International Journal of Primatology* 10(6): 595-606.

Sauther, M . L. (1991) *The effect of reproductive state, social rank, and group size on resource use among free-ranging ringtailed lemurs (Lemur catta) of Madagascar*. Ph.D. thesis, Washington University, St. Louis, MO.

Sauther, M. L. (1992) Effects of reproductive state, social rank, and group size on resource use among free-ranging ringtailed lemurs (*Lemur catta*) of Madagascar. Ph.D. dissertation, Washington University, St. Louis, MO.

Sauther, M. L. & Sussman, R. W. (1993) A new interpretation of the organization and mating systems of the ringtailed lemur *(Lemur catta)*. In: *Lemur Social Systems and their Ecological Basis* (eds. P. M. Kappeler, J. Gazehorn). New York: Plenum Press, pp 11-121.

Sauther, M. L., Sussman R.W., & Gould L. (1999) The socioecology of the ringtailed lemur: thirty-five years of research. *Evolutionary Anthropology* 8(4): 120-32.

Sbeglia, G. (2009) The relationship between social behavior and food, proximity, kinship, and previous agonism in two ringtailed lemur social groups. In: *Patterns of affiliation and agonism in a ringtailed lemur, Lemur catta, society: Tests of the socioecological model and other hypotheses*. Master's thesis, University of Missouri – St. Louis, pp 36-105.

van Schaik, C. P. (1989) The ecology of social relationships amongst female primates. In: *Comparative Socioecology: The Behavioural Ecology of Humans and Other Animals* (eds. V. Standon and R. A. Foley)*.* Oxford: Blackwell Publishing, pp. 195-218.

Schino, G. (1998) Reconciliation in domestic goats. *Behaviour* 135: 343–356.

Silk, J. B. (1997) Social components of fitness in primate groups. *Science* 317: 1342-1351.

Silk, J. B. (2002) The form and function of reconciliation in primates. *Annual Review of Anthropology* 31:21-44.

Sterck, E. H. M., Watts, D. P. & van Schaik, C. P. (1997) The evolution of female social relationships in nonhuman primates.   *Behavioral Ecology and Sociobiol*ogy 41: 291-309.

St. Louis Zoo (2007) Documents provided by staff. St. Louis, MO.

Sussman (1991) Demography and spatial organization of free-ranging *Lemur catta* in the Beza Mahafaly Reserve, Madagascar. *American Journal of Physical Anthropology* 84: 43-58.

Sussman, R. W. (1992) Male life history and intergroup mobility among ringtailed lemurs (*Lemur catta*). *International Journal of Primatology* 13: 395-413.

Sussman, R. W., Andrianasolondraibe, O., Soma, T. & Ichino, I. (2003) Social behavior and aggression among ringtailed lemurs. *Folia Primatologica* 74: 168-172.

Sussman, R.W., Garber, P. A., & Cheverud J. M. (2005). Importance of Cooperation and Affiliation in the Evolution of Primate Sociality. *American Journal of Physical Anthropology*. 128: 84-97.

Taylor, L. (1986) Kinship, dominance, and social organization in a semi-free ranging group of ringtailed lemurs (*Lemur catta)*. Ph.D. Dissertation. Washington University, St. Louis, MO.

Taylor, L. & Sussman, R. W. (1985) A preliminary study of kinship and social organization in a semi free-ranging group of *Lemur catta*. *International Journal of Primatology* 6: 601-614.

de Vries, H. (1995) An improved test of linearity in dominance hierarchies containing unknown or tied relationships. *Animal Behaviour* 50: 1375-1389.

de Waal, F. B. M. (1989) *Peacemaking Among Primates*. Cambridge: Harvard University Press.

de Waal, F. B. M. & van Roosmalen, A. (1979) Reconciliation and consolation among chimpanzees. *Behavioral Ecology and Sociobiology* 5: 55–66.

Wahaj, S. A., Guse, K. R. & Holekamp, K. E. (2001) Reconciliation in the spotted hyena (*Crocuta crocuta*). *Ethology* 107: 1057–1074.

Wittig, R., M. & Boesch, C. (2003) Food competition and linear dominance hierarchy among female chimpanzees of the Tai National Park. *International Journal of Primatology* 24(4): 847-867.

Wittig, R. M., Crockford, C., Wikberg, E., Seyfarth, R. M., & Cheney, D. L. (2007) Kin-mediated reconciliation substitutes for direct reconciliation in female baboons. *Proceedings of the Royal Society B*. 274: 1109-1115.

Wright, P. (2008) Decades of research and conservation: The Elwyn Simons influence. In: *Elwyn Simons: A Search for Origins* (eds. J.G. Fleagle and C.C. Gilbert). Springer: New York.